Individual differences in the dynamics of collinear facilitation?

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ABSTRACT

Collinear facilitation refers to the increase in sensitivity found for a target when aligned between nearby, brighter flankers. Many studies have explored the spatial and temporal aspects of this arrangement, and there is a consensus that two mechanisms could be responsible for this phenomenon; lateral excitation within V1 and extra-striate feedback to V1. There is some debate as to whether facilitation can still occur if the target is presented before the flankers, a manipulation known as backward masking, which could rely on feedback to V1. We shed light on this debate by using forward, simultaneous and backward masking with a relatively large sample of 26 participants. We used short stimulus presentation times (35 ms) and a range of SOAs (stimulus onset asynchronies) (−70, −35, 0, 35 and 70 ms) in order to isolate any feedback facilitation that may occur. We found that collinear facilitation occurred with forward masking (+ve SOAs) in all participants. However, facilitation with backward masking (−ve SOAs) only occurred in 54% of participants. We present a basic model of facilitation that simulates the results of our experiment and could account for differences between previous studies. The model indicates that facilitation with backward masking arises primarily from feedback excitation. Our findings suggest that both lateral connectivity and extra-striate feedback contribute to target facilitation, but in fundamentally different ways and that feedback may be significantly reduced in some participants.

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1. Introduction

Over the last twenty-five years, the vertical Gabor triplet (Fig. 1B) has featured in many psychophysical investigations concerning the nature of contextual interactions between orientation selective neurons in the primary visual cortex (V1). Since Polat and Sagi (1993) first demonstrated both facilitation and suppression with such an arrangement, a multitude of spatial (Freeman, Sagi, & Driver, 2001, 2004; Giorgi et al., 2004; Huang, Chen, & Tyler, 2012; Huang & Hess, 2007, 2008; Huang, Hess, & Dakin, 2006; Jachim et al., 2015; Katkov & Sagi, 2010; Kéita et al., 2011; Lev & Polat, 2011; Mizobe et al., 2001; Polat, 2009; Polat & Sagi, 1994, 2007; Polat et al., 1998, 2005; Shani & Sagi, 2005; Sterkin, Sterkin, & Polat, 2008; Woods, Nugent, & Peli, 2002; Wu & Chen, 2010; Zenger-Landolt & Koch, 2001) and temporal (Cass & Alais, 2006; Huang & Hess, 2008; Li et al., 2010; Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007; Sterkin, Yehezkel, & Polat, 2012; Sterkin & et al., 2009; Tanaka & Sagi, 1998) combinations of target and flanker designs have been developed.

One of the key parameters determining whether interactions are facilitatory or suppressive is the distance between the target and flanking Gabors. This distance is usually expressed in terms of the wavelength (λ) of the Gabor (the combined width of a single dark and light stripe), and Polat and Sagi (1993) demonstrated suppression when this distance was less than 2λ. At these short distances, and depending on the spatial frequency of the stimuli, there may be some spatial overlap between the target and flanking Gabors. This suppression, known as overlay suppression (Bonds, 1989; Carandini, Heeger, & Movshon, 1997; DeAngelis et al., 1992; Morrone, Burr, & Maffei, 1982) is thought to be the result of lateral inhibition as the flanking Gabors stimulate inhibitory neurons in the vicinity of the target Gabor (Macknik & Martinez-Conde, 2007). As target-to-flanker separation increases, suppression turns to facilitation, with optimal facilitation occurring at a separation of 3λ. Although facilitation decreases as separation increases beyond 3λ, it is still apparent at separations of 12λ (Polat & Sagi, 1993). These contextual, facilitatory interactions are thought to be mediated by intrinsic horizontal (lateral) connections in V1 (Gilbert & Wiesel, 1983, 1989; Livingstone & Hubel, 1984; Polat & Sagi, 1993; Rockland & Lund, 1982) and/or feedback to V1 from higher cortical areas (Angelucci et al., 2002; Freeman et al., 2003; Huang & Hess, 2008; Hupe et al., 1998). This paper will
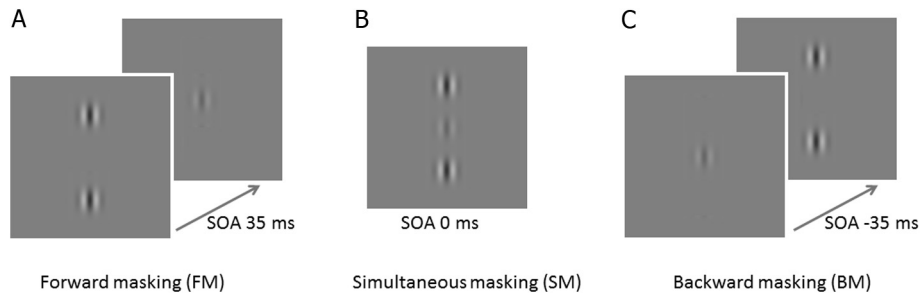
Fig. 1. Presentation sequence of target and flankers for the different masking arrangements. (A) With forward masking the target is presented after the flankers. (B) With simultaneous masking the target is presented at the same time as the flankers. (C) With backward masking the target is presented before the flankers. Note that backward masking is distinguished from forward masking by a negative SOA.

focus on studies using a target and flanker separation of 3λ, with the assumption being that interactions at these distances are largely facilitatory rather than suppressive.

The temporal properties of collinear facilitation are less well investigated than its spatial properties. The majority of investigations into collinear facilitation have used simultaneous masking (SM, stimulus onset asynchrony (SOA) = 0 ms (Fig. 1B)) in which the target and flankers are displayed simultaneously and have identical presentation times. This temporal arrangement has consistently shown facilitation when target separation is greater than 2λ. Facilitation has also been shown when the flankers are displayed before the target (forward masking, FM, SOA > 0 ms (Fig. 1A)) (Li et al., 2010; Polat & Sagi, 2006; Polat et al., 2007; Tanaka & Sagi, 1998). However, experiments with the reverse temporal configuration, i.e. in which the target is displayed before the flankers (backward masking, BM, SOA < 0 ms (Fig. 1C)) have delivered mixed results (Huang & Hess, 2008; Polat & Sagi, 2006; Sterkin et al., 2009).

The temporal characteristics of mechanisms responsible for facilitation will depend upon the dynamics of underlying neural excitatory connections. Two different types of excitation – driving and modulating are thought to contribute to facilitation at the target site in V1. Feed-forward stimulus-driven excitation is a fast-onset and transient *driving* influence that can cause the target neurons to fire. This is in contrast to the slow-onset and sustained *modulating* influence of the horizontal excitation, which makes target neurons more susceptible to firing (Sherman & Guillery, 1998; Spratling, 2013). In addition, it has been shown that feedback excitation to V1, long assumed to have a modulating influence, can also have a driving influence (Covic & Sherman, 2011; De Pasquale & Sherman, 2011). Examining facilitation with FM and BM is important because they are thought to rely on different mechanisms, FM making use of lateral connections, and BM making use of feedback connections (Huang & Hess, 2008). We suggest that lateral connectivity plays little part in facilitation with BM for short duration stimuli, since the modulating influence of the horizontal connections would arrive at the target site after target activation has ceased.

Polat and Sagi (2006) conducted a series of experiments examining the effect of different temporal masks on collinear facilitation. Using a two interval forced choice (2IFC) design, they presented target and flankers at a wide range of spatial separations (2λ –12λ) and a variety of temporal configurations, including FM, SM and BM. For FM and SM they found typical patterns of facilitation i.e. suppression at separations that were less than 2λ, maximum facilitation at 3λ, and a reduction in facilitation as separation increased. However, in the BM condition, facilitation was not evident at any separation including 3λ. They also presented a descriptive model of collinear facilitation mediated by lateral connections in V1. In a further study of the temporal

properties of collinear interactions involving both psychophysical and visually evoked potential (VEP) experiments, Polat et al. (2007) examined the effect of FM, SM and BM on target and flanking Gabors at separations of 2λ and 3λ. Their results echoed those of the previously described study, with facilitation found for FM and SM, but not for BM. In each of these studies, the display duration of the target and the flanking pair was 60 ms and, in the BM condition, the target was presented 120 ms before the flankers. Polat and colleagues interpret these results as an indication that collinear facilitation relies predominantly on lateral connections and that, in the case of BM, horizontal connections cannot enhance a target that is no longer active (Fig. 2A).

However, in a later study examining the dynamics of collinear facilitation, Huang and Hess (2008) demonstrated significant BM facilitation in a 2IFC design with target and flanker separations of 3λ. The presentation time of their target and flankers was 50 ms, and facilitation was measured over a range of SOAs that included FM, SM and BM at multiples of 50 ms. Peak facilitation was estimated to occur when the target preceded the flankers by 30 ms (BM). No significant facilitation was found when the target-to-flanker SOAs exceeded ±150 ms. Huang and Hess suggest that collinear facilitation cannot rely on horizontal connections alone, but may also involve a rapid, orientation specific interaction based on feedback connections from V2 (Girard, Hupe, & Bullier, 2001) (Fig. 2B).

The primary difference in the methods used by Polat and colleagues compared to Huang and Hess was the length of SOA. In order for feedback facilitation to occur, the target and flanker sites in V1 must be activated simultaneously (Angelucci et al., 2002; Cass & Alais, 2006; Huang & Hess, 2008). This 'window of integration' is dependent on the SOA and the fact that lower-contrast target signals take longer to reach V1 than higher-contrast flanker signals, a phenomenon known as contrast dependent onset latency (CDOL) (Reich, Mechler, & Victor, 2001; Sestokas & Lehmkuhle, 1986). For these reasons we suggest that Polat et al. may have used SOAs that were too long to allow-BM to occur (Fig. 2B). A long BM SOA would mean that the target site was stimulated before the flanker sites, despite the fact that, due to CDOL, low-contrast target signals arrive later in V1 than the higher contrast flanker signals. Consequently, we suggest that the *target delay* (TD), i.e. the extra time it takes for target signals to reach V1 compared to flanker signals (Fig. 2) is the key to understanding the differences in previous findings.

In the current study, we investigate the temporal dynamics of collinear facilitation in a relatively large group of adults (N = 26 compared to previous studies reported above that used 3–5 participants). We varied the SOA between target and flanking Gabors separated by a distance of 3λ. We used SOAs that were shorter than those used by Polat and colleagues (−70 ms, −35 ms, 0 ms, 35 ms and 70 ms), and expected to find facilitation for all temporal condi-